NESTING BIOLOGY OF *DOLICHOVESPULA NORVEGICOIDES* (HYMENOPTERA: VESPIDAE)[1]

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ABSTRACT: *Dolichovespula norvegicoides* inhabits very moist areas. Colonies were much larger than those previously collected with nests of 3 to 5 combs, 701 to 1,641 cells, and 137 to 321 workers. Estimates on adult production at normal colony death ranged from 562 to 2,896. The nests were unusual in that reproductive cells were sometimes constructed on all combs. Nest associates *Sphecophaga vesparum burra*, *Vitula edmandsae serratilineela*, earwigs, and possibly *Triphleba lugubris* were collected.

Dolichovespula norvegicoides (Sladen) is a rarely collected species, with little known about its biology and behavior. Distribution is restricted almost entirely to the Canadian and Hudsonian zones of the Boreal Region (Akre *et al.* 1981, fig. 41).

Previous collections of *D. norvegicoides* nests included one by Bequaert (1931), one by Akre *et al.* (1981), and three by Akre and Bleicher (1985). The three nests described in 1985, all with no more than 31 workers, 3 combs (n=2), and 263 cells (n=2), were found in Alaska, Idaho, and Maine (Akre and Bleicher 1985). Two were supraterrestrial (half buried in the soil), and one was constructed inside a log.

The purpose of this paper is to report on seven additional colonies/nests collected in the state of Washington.

MATERIALS AND METHODS

The seven colonies of *D. norvegicoides* were collected in the western half of Cowlitz County, WA between 1986-1992. All colonies were considered mature in that the production of reproductives was underway in the nest. The colonies were located by homeowners who phoned in requests for removal, thus collections were biased towards larger colonies in urban areas.

During collection, flying individuals, typically workers, were vacuumed or netted and transferred to the vacuum, and the nest was placed in a plastic bag. Carbon dioxide was used to quiet the workers if necessary, and the colony was frozen as soon as possible for later analysis. The number of individuals that could not be collected but were left

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behind at the site was estimated and noted.

Colony analyses included counting adults, combs, and cells. Cells were tallied as containing one egg, more than one egg, larvae (3 general sizes; small, medium, large); those having caps, and empty. In addition, cells were examined for parasites. Observations were also made of habitat, nest support, envelope paper, combs, and buttressing.

Estimates were made of the number of adults that had emerged at the time of collection, and the number that would have been produced by the colony before natural demise if it had not been collected. Production at the time of collection was calculated by counting the silk layers left behind in the cells by the pupae that emerged as adults. A minimum and maximum adult production at natural colony demise were calculated to give a range of the estimated total production of the colony. The minimum was calculated by adding the number of capped cells to production at collection, since most pupae emerge even after all the adults die. The maximum was calculated by adding the number of all occupied cells to production at collection.

RESULTS AND DISCUSSION

Colonies were numbered chronologically as collected. The first nest (#1) was collected on 27 July 1986, when the colony was essentially dead. *Dolichovespula arenaria* (F.) colonies found nearby were approximately one month ahead of their "normal" colony schedule on this date, indicating that this was an unusual year; very warm weather early allowed most yellowjackets to develop colonies much earlier than normal. The other six colonies were collected at or near their peak population levels on 15 July 1989 (# 2), 27 July 1989 (#3), 10 July 1990 (#4), 16 June 1992 (# 5), 18 June 1992 (# 6) and 7 July 1992 (#7).

Habitat. Collection areas were moist (ca 100 cm or 40 in. ppt annually) and were located near rivers and streams. Elevations ranged from 30-570 m. Six of the seven colonies had nests located low in shrubs, including rhododendron, salal, azalea, salmonberry, blackberry, and/or huckleberry. Three were 30-34 cm from the ground, one was 133 cm high, the remaining two touched the ground. One of the latter was supraterrestrial, as the nest penetrated the leaf litter layer where the workers excavated debris. Soil was probably not excavated. The seventh colony (#1) was collected from the mossy crotch of a bigleaf maple tree 6.7 m above ground. Approximately half of the nest was under the moss layer, and one-third of the envelope was discontinuous where the nest contacted the trunk. The moss layer was probably pulled away from the tree as the nest expanded. All nests had leaves and twigs or moss incorporated into

the envelopes. Leaves, smaller twigs, and moss were chewed away on the inside of the envelope.

Diameters of initial support twigs of the other nests ranged from 2-10 mm, (x =5.8 mm, n=6: nest #1 support unknown).

Nest Construction. The envelope paper was laminar, but the layers were thinner than those of *D. maculata* (L.) or *D. arenaria.* Akre and Bleicher (1985) noted that the paper weave was looser and consisted of smaller fibers. This was also true of the envelope of these nests. The envelope paper color on all nests was grey with subtle variations from lighter to darker grey, with occasional stripes of brown-grey, yellow-grey, red-grey, or green-grey paper. Differences in color variations was much less than that seen in envelope paper of either *D. maculata* or *D. arenaria.*

Nests had an average of 24.5 layers of envelope on the top where the inner layers had not been cut away or modified for nest enlargement [range (r) =22-29, n=6; envelope from nest # 5 was not included as it was smashed]. Layers on the sides of the nests averaged 8.2 (r=6-14, n=13). Two counts were made of the envelopes on different sides of each nest except for nest #5, where only one count was made because of envelope damage. These counts on opposite sides differed by an average of 3.3 layers (r=0-8, n=6).

Nest #4 had an irregular envelope and possible comb irregularities due to comb separations, but since this colony was the second largest, the damage apparently caused minimal disruption to the colony. Due to the damage, additional envelope was formed between combs 2 and 3, and a layer of previous envelope had folded inward between combs 3 and 4. While other active colonies had from 1-10% empty cells, this colony had 24% of the cells empty, some cells were cut down, and there were areas where envelope was built over the cells (Cells covered with envelope also occur normally in colonies in decline). Combs 1, 4, and 5 were normal, while combs 2 and 3 had 140 and 32 cut down cells, respectively. Comb 3 was unusual as there was one large larva, 2 small larvae, and 62 egg or empty cells from which adults had already emerged among large numbers of cells capped for the first time. Cut down cells were found in small numbers in one other nest (nest # 1), and this was considered normal in the nest sequence.

The queen pedicels of the top combs of all the nests were glazed (secretions from the queen), and the tops of these combs were shinier than the lower combs. The paper of the original queen comb was yellow-grey in two nests (#5 and #2) and grey surrounded by yellow-grey, then becoming normal grey in one nest (#7). The top combs of the remaining nests were uniform grey.

Ribbon buttressing was found on all combs of all nests except for the small bottom combs. Nests had an average of 46.2 cm of ribbon on all combs (r=4.8-84.0 cm). The top comb usually had about a quarter of all buttressing (x=24.7%, r=6-48%), while combs two and three had the greatest amount of buttressing (comb 2: x=34.9%, r=12-77%; comb 3: x=36.0%, r=26-56%, n=6). Combs 4-5 had little buttressing as they were constructed just prior to collection. Colony # 1, which was in advanced decline at collection, had fairly even amounts of buttressing on all combs (comb 1: 32%, comb 2: 18%, comb 3: 31%, comb 4: 19%; 84 cm total buttressing). In most cases 1-4 ribbons radiated outward from the central pedicel (x=75.6% ribbon on all combs). Some separate ribbons occurred on the sides of the cells (x=10.9%, mostly on comb 1; attached to the envelope above), and a few isolated ribbons were neither attached to the center peticel nor on the sides of the cells (x=13.6%, usually on middle combs).

Twenty mature (full length) cells were measured on each comb to the nearest 0.1 mm. Cell measurements were not taken from six of the reproductive combs as all the cells were immature, or from nest # 1 which was totally destroyed searching for parasites. Twenty measurements of cells were taken from the queen and the worker sections of the first comb of nest # 6, but queen cells on comb 1 of nest #4 were not included in measurements as there were very few cells. Worker cells averaged 4.8 mm diam (r=4.1-6.5 mm, n=120 cells from 6 combs), and reproductive cells averaged 6.4 mm diam (r-5.1-8.0 mm, n=300 cells from 15 combs).

Comb Contents: The nests had 3 to 5 combs, with an average of 4.3 combs (n=7, Table 1). The top comb (comb 1) consisted of smaller cells producing first workers, then males; while the remaining combs were made of larger reproductive cells producing males and queens. At the time of collection the capped cells of comb 1 in the nests of the 6 living colonies contained both male and worker pupae. *D. norvegicoides* is unusual as queen cells are found on the edge of the worker comb. This has not been reported previously for any member of the genus *Dolichovespula.*

Three of the seven nests had queen cells on their first worker comb. Colony #6 had 88 large cells on the edge of the worker comb, consisting of 58 capped cells and 30 non-capped cells. Fifty five of the capped cells contained queen pupae and three contained male pupae. Comb 1 of nest #4 had three large cells; queens had emerged from two, and one contained a queen pupa. Comb 1 of colony # 1 had 6 empty reproductive cells from which queens had emerged.

Worker combs (comb 1) consisted of an average of 317 cells (r= 218-405 cells, n=7). An average of 37% of these contained eggs (r=18-52%, n=6 excluding colony #1), 22% larvae (r=17-29%, n=6), 36% pupae (r=27-50%, n=6), and 5% were empty (r=1-9%, n=6). The larvae were evenly divided among small (33.4% of all larvae, 6 colonies), medium (30.5%), and large larvae (36.1%).

The reproductive combs had an average of 968 cells (r=331-1,280 cells, n=7). An average of 27% of the cells contained eggs (r=19-43%, n=6 excluding colony # 1), 31% larvae (r=24-40%, n=6), 32% pupae (r=24-39%, n=6), and 10% were empty (r=2-30%, n=6). One third of all the larvae in the 6 colonies were small, and there were slightly more medium (37.6%) than large larvae (29.3%).

Cells that contain more than one egg or small larva indicate colony decline as workers begin to lay eggs due to loss of queen control. Five of the six living colonies had multiple eggs and/or small larvae per cell: #4 (42 cells), #6 (9), # 5 (8), #7 (38), and #3 (5).

Adults and Adult Production. The foundress was collected with five of the six active colonies (Table 2). Only one had age spots (Ross 1984) typical of old foundresses of other species. Some had darker areas on the yellow tergal bands of the gaster, but these were not age spots, and several new queens had similar markings. Foundresses without age spots were distinguished from new queens by the lack of hair and slightly frayed wings. In addition, the wings of foundresses were tinted yellow-brown, while new queens had smoky-grey wings.

The six active colonies contained an average of 213 workers (r=137-326), 25 males (r=7-71), and 28 new queens (r=0-57); only one colony, #7, did not have new queens (Table 2).

The number of adults produced to date of colony collection was based on number of silk pupal layers left in cells by emerging adults (Table 3). The majority of the cells in the six live colonies had not yet produced any adults (r=45-75% of cells) while only 12% of the nearly dead colony (#1) cells had never produced adults. Seventeen to 41% of cells from the six living colonies had produced one adult each, while 71% of colony #1 cells had produced one adult. Few cells from the 6 living colonies had produced 2 or more adults per cell (r=6-19), and this was also true for colony #1 where 16% of the cells produced 2 adults per cell.

An average of 805 workers, queens, and males (range: 330-1,398) had been produced from the six active colonies at the time of collection (Table 4). Possible errors in this calculation include pupae that died and were removed from the capped cells. The average minimum number of adults that may have been produced at natural colony death was 1,119

(r=562-1,998). The average maximum number of adults was 1,834 (r=1,075-2,896). Possible errors in the estimate of the maximum population include the possibility of colony death before the cell occupants reached maturity. Also, eggs that had not been laid at the time of collection might have developed into adults if the colony had not been collected. However, comparisons of the six active colonies with cell usage in colony #1 indicated that the range was accurate, and that the maximum end of the range was probably more accurate than the minimum. The number produced by colony #1, a smaller colony, by its natural demise was 1,457.

Parasites and Associates. *Sphecophaga vesparum burra* Cresson is a parasite that occurs in colonies of *D. arenaria* (Greene *et al.* 1976), *D. maculata* (Akre and Myhre 1991), and *D. saxonica* (F.) (Edwards 1980). It was found in high numbers in colony #1. A total of 22 white and 49 yellow (overwintering) cocoons was found in the combs of this nest. Nine white and 18 yellow cocoons were found in comb 1, 7 yellow in comb 2, 2 white and 10 yellow in comb 3, and 11 white and 14 yellow in comb 4.

Vitula edmandsae serratilineela Ragenot, a pyralid scavenger typically found in dead and dying *D. maculata* and *D. arenaria* nests, was found in nest #1. Diptera larvae, tentatively identified as the phorid

Table 1. Cell contents of colonies in chronological order as collected.

Colony No.	Date Collected	Comb Type	No. Combs	No. Cells	No. Eggs	Larvae small	Larvae medium	Larvae large	Capped Cells	# Empty (% Empty)
1	27/VII/86	Worker	1	261	0	0	0	0	0	261(100)
		Queen	3	1,119	0	0	1	0	0	1,118(100)
		TOTALS:	4	1,380	0	0	1	0	0	1,379(100)
2	15/VII/89	Worker	1	405	78	36	34	47	178	32(8)
		Queen	4	1,082	324	151	127	101	322	57(5)
		TOTALS:	5	1,487	402	187	161	148	500	89(6)
3	27/VII/89	Worker	1	361	160	25	21	14	107	34(9)
		Queen	4	1,280	307	132	122	117	493	109(9)
		TOTALS:	5	1,641	467	157	143	131	600	143(9)
4	10/VII/90	Worker	1	314	154	28	16	25	85	4(1)
		Queen	4	1,203	232	66	136	87	326	356(30)
		TOTALS:	5	1,517	386	94	152	112	413	360(24)
5	16/VI/92	Worker	1	218	86	20	12	11	79	10(5)
		Queen	3	928	262	54	109	68	334	101(11)
		TOTALS:	4	1,146	348	74	121	79	413	111(10)
6	18/VI/92	Worker	1	287	51	19	30	27	144	16(6)
		Queen	3	831	157	142	116	75	288	53(6)
		TOTALS:	4	1,118	208	161	146	102	432	69(6)
7	7/VII/89	Worker	1	370	193	19	21	35	99	3(1)
		Queen	2	331	142	20	31	52	80	6(2)
		TOTALS:	3	701	335	39	52	87	179	9(1)

Triphleba lugubris (Meigen), were found in cells with reddish tinted caps in nests #1 (one in each of six cells), #4 (1 in one cell, 2 in a second), and #2 (3 in one cell). The capped cells each contained 1-3 larvae, and the yellowjacket pupae were dead but usually intact. The largest maggot we found had burrowed into the abdomen of a pupa (# 4). Earwigs were found in colonies # 5 and #6.

D. adulterina (du Buysson) parasitizes colonies of *D. norvegicoides* (Wagner, cited by Yamane 1975), but none was found in these colonies.

Table 2. Number of old queens (foundresses if not usurped), workers, new queens, and males collected with colony. Colony # 1 was not included in averages as it was essentially dead.

Colony Number	Date Collected	Old Queens	Workers	New Queens	Males
2	15/VII/89	1	288	18	17
3	27/VII/89	0	205	48	71
4	10/VII/90	1	326	14	17
5	16/VI/92	1	137	57	21
6	18/VI/92	1	141	28	15
7	7/VII/89	1	183	0	7
	Ave:	0.8	213.3	27.5	24.7
1	12/VII/86	0	22	0	1

Table 3. Cell usage by emerged adults based on number of silk pupal layers in cells.

Colony Number	No.Cells in Nest	No. cells used: (% of total cells)				
		0 times	1 time	2 times	3 times	4 times
1	1,380	168 (12)	984 (71)	211 (15)	17 (1)	0
2	1,487	1,118 (75)	275 (18)	68 (5)	26 (2)	0
3	1,641	744 (45)	560 (34)	196 (12)	118 (7)	23 (1)
4	1,517	786 (52)	542 (36)	145 (10)	39 (3)	5 (0.3)
5	1,146	553 (48)	474 (41)	86 (8)	33 (3)	0
6	1,118	862 (77)	191 (17)	56 (5)	9 (1)	0
7	701	403 (57)	223 (32)	65(9)	10 (1)	0

Table 4. Total adult production and number of adults produced per cell up to time of collection ("At Collection Date"), and estimated total production and number produced per cell if colony had not been collected ("Natural Death").

Colony Number	At Collection Date		Natural Death	
	Total Production	# Produced per Cell	Total Production Min.-Max.	# Produced/cell Min.-Max.
2	489	0.33	989-1,887	0.67-1.27
3	1,398	0.85	1,998-2,896	1.22-1.76
4	969	0.64	1,382-2,126	0.91-1.40
5	745	0.65	1,158-1,780	1.01 -1.55
6	330	0.30	762-1,379	0.68-1.23
7	383	0.55	562-1,075	0.80-1.53
Ave:	719	0.55	1,142-1,857	0.88-1.46
1	1,457	1.06	1,457	1.06

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